Topographic representations of object size and relationships with numerosity reveal generalized quantity processing in human parietal cortex

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Humans and many animals analyze sensory information to estimate quantities that guide behavior and decisions. These quantities include numerosity (object number) and object size. Having recently demonstrated topographic maps of numerosity, we ask whether the brain also contains maps of object size. Using ultra-high-field (7T) functional MRI and population receptive field modeling, we describe tuned responses to visual object size in bilateral human posterior parietal cortex. Tuning follows linear Gaussian functions and shows surround suppression, and tuning width narrows with increasing preferred object size. Object size-tuned responses are organized in bilateral topographic maps, with similar cortical extents responding to large and small objects. These properties of object size tuning and map organization all differ from the numerosity representation, suggesting that object size and numerosity tuning result from distinct mechanisms. However, their maps largely overlap and object size preferences correlate with numerosity preferences, suggesting associated representations of these two quantities. Object size preferences here show no discernable relation to visual position preferences found in visuospatial receptive fields. As such, object size maps (much like numerosity maps) do not reflect sensory organ structure but instead emerge within the brain. We speculate that, as in sensory processing, optimization of cognitive processing using topographic maps may be a common organizing principle in association cortex. Interactions between object size and numerosity maps may associate cognitive representations of these related features, potentially allowing consideration of both quantities together when making decisions.

object size | numerosity | topographic maps | high-field 7T fMRI

Humans and animals share a sense of numerosity (object number) that guides behavior and decisions (1, 2), for example choosing numerous objects when foraging or shopping. As such, numbers and numerical processing are fundamental to cognitive neuroscience and are linked to mathematics, value judgments, and economics (1, 3). Because aspects of numerosity perception mirror primary sensory perception, it has been referred to as a "number sense" (4). However, another theory (5) sees numerosity as one aspect of a more generalized quantity system. Here we investigate the representation of another quantity: object size.

Behaviorally, object size and numerosity perception interfere with each other (6). At the neural level, single neurons in macaque parietal cortex can be tuned to numerosity (7), line length (a measure of object size), or both (8). However, it is unclear whether numerosity and object size preferences are related, either in the same neurons or in nearby neurons (8). Using human neuroimaging, we have shown that numerosity-tuned neural populations in human posterior parietal lobe are topographically organized (9): Similar numerosity preferences are grouped together, changing gradually across the cortical surface. Visual features of the presented stimuli affect numerosity preferences, which may reflect preferences for particular object sizes (9, 10).

Here we ask whether object size-tuned responses are found in the same area, whether these are topographically organized, and how tuning and organization relate to representations of numerosity and visual space in the same area. We find topographically organized object size-tuned responses that largely overlap with numerosity maps and show correlated tuning preferences. However, many differences between object size and numerosity tuning and map organization suggest that responses arise from distinct mechanisms.

These intermingled neuronal representations of object number and size may allow generalization and abstraction in quantity processing and consideration of related quantities when making decisions. Optimization of cognitive processing using topographic maps may be a common organizing principle in association cortex, particularly in quantity processing, as it is in sensory processing.

Materials and Methods

We showed a single object (a circle) whose size varied systematically within a 7T functional (f)MRI scan (Fig. 1A, Fig. 1C, *Top*, and *SI Materials and Methods*). We recorded responses to two different stimulus sets on different days. The first ("variable step") allowed any object placement where the entire object lay within 0.75° of fixation. Here, larger objects had a more limited range of possible positions, and so took smaller average steps between consecutive placements (Fig. 1A). The second condition ("constant step") always used the same step length between consecutive object locations, in random directions. These two conditions gave very similar responses, demonstrating repeatability, and are averaged for most analyses. Subjects

Significance

Processing of quantities such as object sizes and numbers relies on analyses of sensory information and informs cognitive tasks such as decision making and mathematics. Whereas sensory processing is organized into topographic maps reflecting sensory organ structure, organization of cognitive processing is poorly understood. We demonstrate topographic representation of object size-tuned responses. This arises separately from object number tuning, but these two quantities are associated in overlapping maps. This generalized quantity representation may allow us to consider object size and number together when making decisions. Optimization of cognitive processing using topographic maps may be a common organizing principle in association cortex, as it is in sensory processing. Linking cognitive representations in maps of related features may support increasingly abstract cognition.
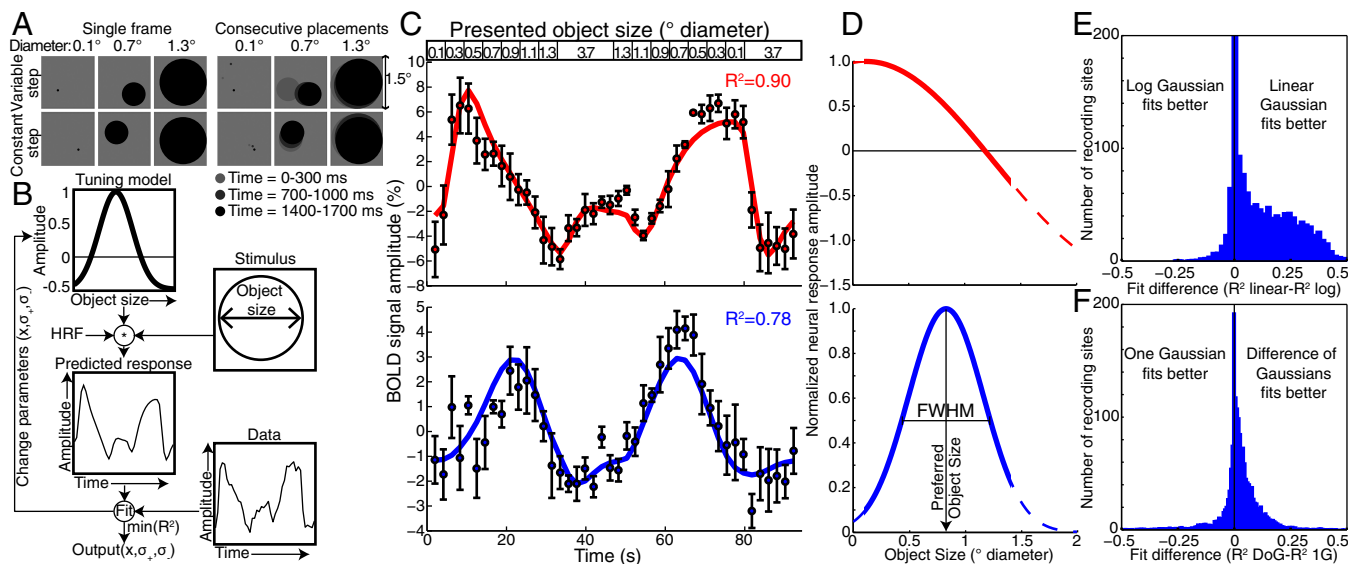
Fig. 1. Stimuli and pRF modeling. (*A*) Example stimuli. Objects were placed either randomly or pseudorandomly to lie entirely within 0.75° of fixation. Using purely random placements, smaller objects can take larger steps between consecutive placements (variable step condition). Therefore, we introduced a condition where objects always made steps of the same length in random directions (constant step condition). These two conditions gave very similar responses. (*B*) pRF modeling procedure (9, 11). A candidate neural tuning model describes a tuning function of an fMRI recording site, characterized by a preferred object size, tuning width, and suppressive surround width. Convolving the tuning model's response amplitude with the time course of presented object sizes and the hemodynamic response function (HRF) predicts the fMRI response for this tuning model. For each recording site, we find the best-fitting tuning model parameters by minimizing the squared difference between the predicted fMRI response and the recorded data. (*C*) Two example fMRI time courses from sites in right posterior parietal cortex, about 2 cm apart, elicited by the presented object size time course (*Top*). Points represent mean response amplitudes; error bars represent the SE over repeated runs. In the *Upper* panel, the largest responses occur after presentation of small objects, whereas in the *Lower* panel the largest responses occur for larger objects, considering the hemodynamic response delay. The tuning model predictions (colored lines) capture over 75% of the variance (R^2) in the time courses. BOLD, blood oxygen level-dependent. (*D*) The tuning models that explain the most variance in each time course. The model describes a linear Gaussian tuning function with a suppressive surround, characterized by two parameters: preferred object size and tuning width summarized by the function's full width at half maximum (FWHM). Different tuning model parameters explain the different responses seen in *C*, capturing similar amounts of variance. Dashed lines show the continuation of tuning functions outside the presented object size range. (*E*) Linear one-Gaussian object size tuning models explain more response variance in most recording sites than logarithmic tuning models. Goodness of fit is evaluated by twofold cross-validation. Comparisons of difference of Gaussian tuning models give similar results. (*F*) Linear DoG object size tuning models explain more response variance in most recording sites than linear one-Gaussian models.

reported when objects were shown in white rather than black (10% of presentations, mean performance 89% correct). No object size judgments were required. Written informed consent was obtained before every scanning session. All experimental procedures were approved by the ethics committee of University Medical Center Utrecht.

Results

Neural Populations in Parietal Cortex Are Tuned to Object Size. These stimuli elicited very different fMRI responses at different recording sites (Fig. 1*C*), which we summarize using object size-tuned population receptive field (pRF) models (Fig. 1 *B–D* and *SI Materials and Methods*) (9, 11, 12). We fit object size tuning as linear difference of Gaussian (DoG) functions that include below-baseline suppressive surround responses. These explained more response variance than logarithmic Gaussian functions (Wilcoxon signed-rank test, $P < 10^{-10}$) or one-Gaussian functions without suppressive surrounds ($P < 10^{-10}$) (Fig. 1 *E* and *F* and Fig. S1*A*) using twofold cross-validation. Nevertheless, our results do not depend greatly on the tuning model chosen.

Object size tuning models summarize the fMRI responses seen using three parameters: (*i*) preferred object size, (*ii*) tuning width, and (*iii*) width of the suppressive surround. They explained the recorded responses well (mean $R^2 = 0.59$, median $R^2 = 0.59$, $P = 0.0016$ after false discovery rate correction) in the posterior parietal area surrounding the previously described numerosity map (9). We only examine tuning properties of recording points with preferred object sizes within the stimulus range. Here, response amplitude decreases on both sides of the preferred object size, demonstrating tuned responses. Recording points with preferred object sizes outside the stimulus range monotonically increase or

decrease their response as we move through the range of object sizes, with no clear evidence of tuning.

Because a circle's area is proportional to its diameter squared, we compare fits from tuning models in linear (diameter, radius, or circumference) and squared (area) space. Tuning functions in linear space explain more response variance than those in square space (Wilcoxon signed-rank test, $P < 10^{-10}$).

Because all objects had the same contrast, display luminance covaried with object size. To distinguish tuning for object size and luminance, we used a control stimulus where the luminance of the object size stimulus was distributed evenly across the largest object in the stimulus set. Responses differed considerably from responses to object size varying stimuli (Fig. S2), so object size-tuned responses do not reflect responses to display luminance.

Topographic Maps of Object Size. We projected each recording site's preferred object size onto the cortical surface around the previously identified numerosity map (*SI Materials and Methods*) (9). This revealed orderly topographic object size preference maps (Fig. 2*A* and Figs. S3 and S4). These were consistently found in similar locations bilaterally on the medial superior parietal lobule (Fig. 2*D*), centered at mean (SD) Montreal Neurological Institute (MNI) x,y,z coordinates −23 (4), −57 (6), 55 (9) and 23 (3), −60 (7), 59 (6) in the left and right hemispheres, respectively.

To quantify this organization, we sorted recording sites within each hemisphere's map by their cortical surface distance from lines of the minimum and maximum object size preferences found in that map. We plotted preferred object size against this distance for each stimulus condition and their average (Fig. 2*B* and Fig. S5). In all subjects, preferred object size increases
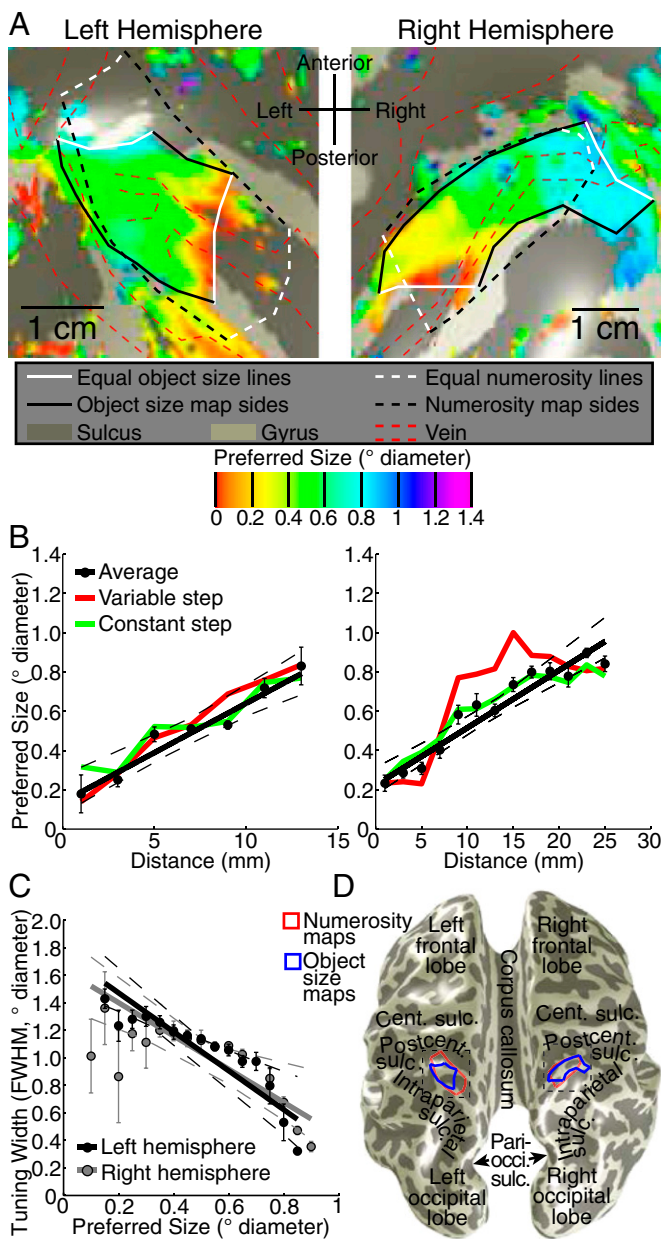
Fig. 2. Topographic representation of object size. (*A*) Object size preferences surrounding the previously described numerosity map (white and black dashed lines) (9) for data averaged from both stimulus conditions. Preferred object size changes gradually between lines of equal minimal and maximal preferred object size (white lines) in both hemispheres, forming topographic maps (black and white solid lines). Areas of low signal intensity, corresponding to pial veins (red dashed lines) (Fig. S3), were excluded from further analysis (21). (*B*) Object size preferences progress approximately linearly along the map. Recording sites were organized by their distances from the white lines in *A*. The two stimulus conditions are shown as colored lines joining condition-specific bin means. (*C*) Tuning width decreases as preferred object size increases. (*D*) Locations of object size and numerosity maps on an inflated cortical surface, relative to nearby major anatomical landmarks. Dashed boxes show the areas detailed in *A*. Cent., central; Pari-occi., parieto-occipital; Postcent, postcentral; Sulc., sulcus. In *B* and *C*, all dots represent the mean in each bin. Error bars represent SEs. All dashed lines represent 95% confidence intervals of the fit (solid line) to the bin means.

significantly and repeatedly across both hemispheres' cortical surfaces, with similar object size preferences found in separate scanning sessions.

Cortical Magnification and Tuning Widths. In these maps, preferred object size increases approximately linearly along the cortical surface (Fig. 2*B* and Fig. S5): Linear functions capture the variance of size preferences with distance as well as more complex logarithmic functions. Tuning widths for object size decrease as preferred object size increases (Fig. 2*C* and Fig. S6).

As such, small object sizes are not overrepresented in comparison with larger sizes, neither by the larger cortical representations nor by the smaller tuning widths seen in the representations of small numerosities, central vision, sensitive somatosensory areas, or dexterous motor areas. Nevertheless, there is a systematic relationship between tuning width and preferred object size.

Relationship to Numerosity Tuning. We measured responses to stimuli of varying numerosity in the same subjects as previously described (*SI Materials and Methods*) (9). These yield very different response time courses than stimuli of varying object size (Fig. S1): The tuning functions that explain most response variance differed considerably between numerosity- and object size-tuned responses. First, object size tuning models describing linear Gaussian functions explain more variance than those describing logarithmic Gaussian functions (Fig. 1*E*). Conversely, numerosity tuning models describing logarithmic Gaussian functions explain more variance than those describing linear Gaussian functions (9). Second, object size tuning models describing DoG functions explain more variance than single-Gaussian functions (Fig. 1*F*). Conversely, numerosity-tuned models describing single-Gaussian functions explain more variance than DoG functions (Wilcoxon signed-rank test, $P < 10^{-10}$). So although we find both numerosity- and object size-tuned responses, the underlying tuning functions are quite different.

Relationship to Numerosity Maps and Visual Field Maps. We found topographic organization of numerosity preferences as previously described (9) (Fig. 3*A*). Numerosity maps were also consistently found in similar locations bilaterally on the medial superior parietal lobule (Fig. 2*D*), centered at mean (SD) MNI x,y,z coordinates of −26 (4), −56 (6), 58 (8) and 22 (2), −61 (3), 60 (6) in the left and right hemispheres, respectively. We quantify our previous finding that numerosity maps were right-lateralized, with less-clear maps in the left hemisphere (Fig. 3*A* and Fig. S7). In all subjects, both the rate of change of numerosity preferences with cortical distance and the interquartile range of numerosity preferences were greater in the right hemisphere than the left (paired t tests, $P = 0.023$ and $P = 0.006$, respectively). For object size preferences, neither the rate of change nor the interquartile range differed significantly between hemispheres ($P = 0.21$ and $P = 0.19$). As such, numerosity maps are significantly right-lateralized, whereas object size maps are similar in both hemispheres.

Although object size and numerosity maps were not coextensive, they partially overlapped in each hemisphere (Fig. 2*A* and Fig. 3*A*). Among recording sites within both maps, numerosity and size preferences are consistently positively correlated (Fig. 3*B* and Fig. S8) in 9 of our 10 hemispheres (Pearson's correlation; Spearman's rank correlation gave similar results). Although smaller object size and numerosity preferences are consistently associated, the ratio of these preferences differs between hemispheres: Any object size is not consistently associated with a particular numerosity.

The direction of greatest object size and numerosity preference change (i.e., direction of map progression) also differed in many hemispheres. In 7 of our 10 hemispheres, the direction of change differed significantly more between object size and numerosity maps than between numerosity maps measured in different sessions. Here, object size preferences increased more posterior-to-anterior than numerosity preferences. However, in the other hemispheres, map directions were very similar.

We characterized the intraparietal sulcus (IPS) visual field maps that partially overlap both object size and numerosity maps (*SI Materials and Methods*) (9) (Fig. 3*C* and Fig. S9). Several results distinguish object size and numerosity preferences from
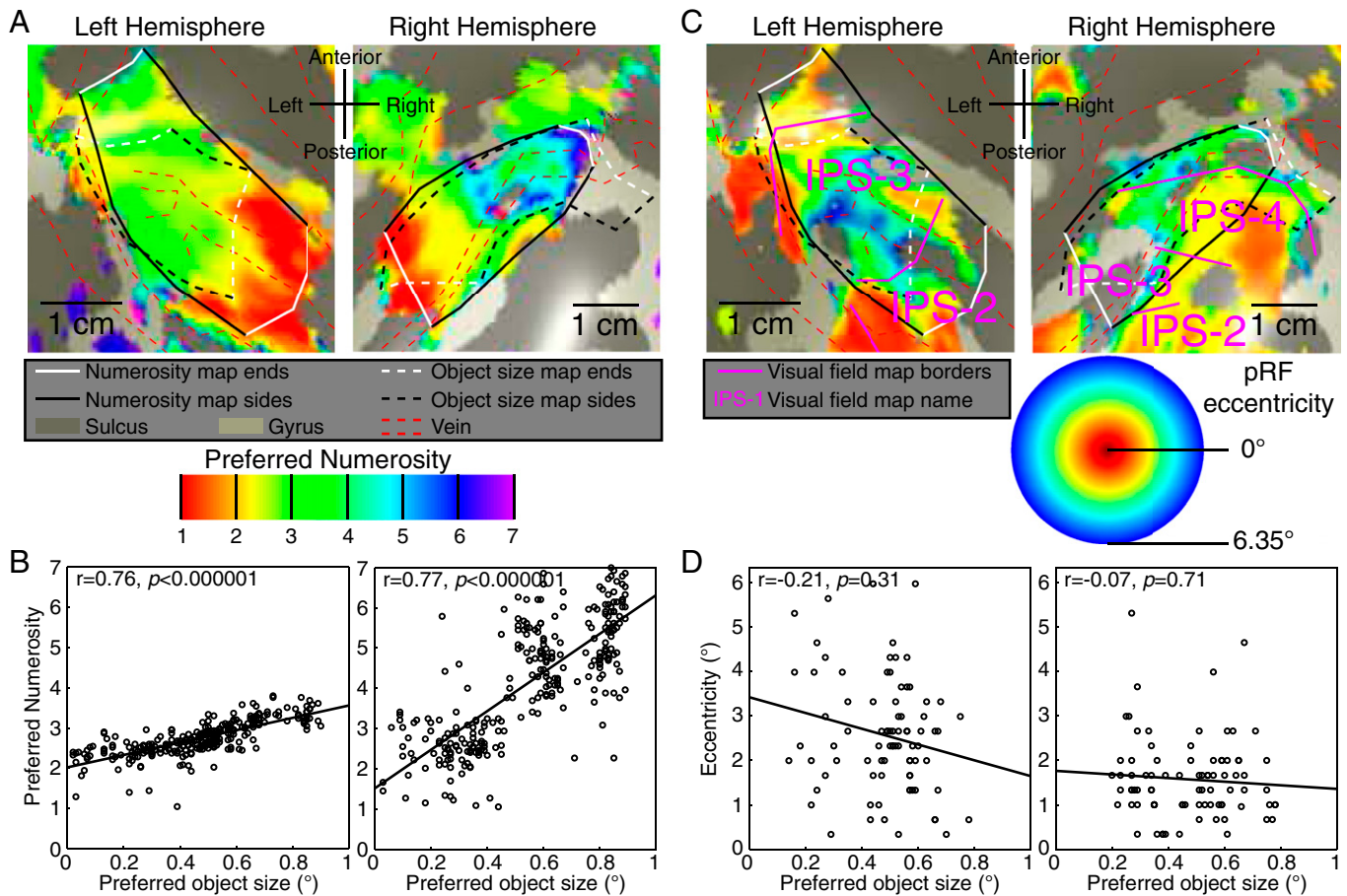
Fig. 3. Relationships between object size maps, numerosity maps, and visual field maps. (A) Numerosity preferences in the same areas as Fig. 2 form numerosity maps (solid black and white lines) that largely overlap with object size maps (dashed black and white lines). Left hemisphere numerosity maps are less clear than right, and represent a smaller numerosity range. Object size maps are similar bilaterally. (B) Among recording sites that lie in both maps, object size and numerosity preferences are correlated. The ratio of these preferences differs between hemispheres. (C) IPS visual field maps partially overlap with object size and numerosity maps. Object size- and numerosity-tuned responses were not limited to the central visual field positions where their stimuli were presented. Visual field map borders did not coincide with object size or numerosity map borders. (D) Among the fewer recording sites that lie in both visual field maps and object size or numerosity maps, neither object size nor numerosity preferences were correlated with pRF eccentricity or pRF size.

visuospatial preferences. (*i*) Object size- and numerosity-tuned responses were not limited to the central visual field positions where we presented their stimuli. (*ii*) Preferred object size is far smaller than pRF size (σ) at the same sites (paired *t* test, $P < 10^{-5}$ in each hemisphere). (*iii*) IPS visual field map borders did not coincide with object size or numerosity map borders (Fig. 3*C*). (*iv*) Visual field map positions relative to object size and numerosity maps varied considerably between subjects and hemispheres. (*v*) Among recording sites within both visual field maps and object size or numerosity maps, neither object size nor numerosity preferences were consistently correlated with visuospatial pRF size or eccentricity (Fig. 3*D* and Fig. S10). However, in the same recording sites, both pRF size and eccentricity are consistently correlated between complementary halves of the visual field mapping data ($P < 0.01$ in 9/10 and 8/10 hemispheres, respectively), demonstrating sufficient data quality to reveal correlations here. (*vi*) Tuning models fit to the presented visual field positions predict responses to our object size stimuli poorly (Fig. S11). As such, object size and numerosity preferences here are not associated with visual field position preferences, pRF sizes, or visual field map locations.

Discussion

We find object size-tuned responses in fMRI recording sites in bilateral human posterior parietal cortex. These show that surround suppression and tuning widths decrease as preferred object size increases. Object size-tuned neural populations form

bilateral topographic maps: Object size preferences progress gradually and approximately linearly across the cortical surface. We characterize numerosity tuning and maps in the same subjects (9). These overlap largely but not completely with the object size maps. Many properties of object size and numerosity representations differ, suggesting they result from distinct mechanisms. However, object size and numerosity preferences were correlated among recording sites within both maps. Although IPS visual field maps partially overlapped with object size and numerosity maps, neither visual field eccentricity nor pRF size correlated with preferred object size or numerosity. As such, this object size tuning is separated from visual field map structure, so its topographic organization emerges within the brain. Object size representations are instead associated with numerosity representations, suggesting that neural processing generalizes across quantities.

Differences Between Object Size and Numerosity Representations. Despite similarities between representations of object size and numerosity, we find many differences in both tuning and cortical organization. First, object size tuning is better-described by linear Gaussian functions, whereas logarithmic Gaussian functions characterize numerosity tuning (7, 9, 13–15). Second, object size tuning widths decrease as preferred object size increases. This contrasts with numerosity tuning widths, which increase with increasing preferred numerosity (7, 9, 14).

What is the functional significance of these differences? Logarithmic numerosity tuning functions have long tails that carry some information about high numerosities, although numerosity preferences above five are rarely seen (9, 15). Object size tuning narrows as preferred size increases, bringing all responses to zero at the top of the presented size range (Fig. 4). Modeled tuning functions can also extend below zero, predicting responses to negative object sizes, which cannot exist. More likely, presenting no object (i.e., zero size) produces no response, truncating the tuning function at zero. So, object size tuning functions seem to be limited at both ends of the presented size range, suggesting that tuning properties might change if different size ranges were presented. Such adaptability may allow us to process a broader range of sizes, much like logarithmic tuning functions increase the effective range of numerosity processing.

A third difference is that object size preferences change approximately linearly with cortical distance, whereas numerosity preferences change more gradually for small numerosities (9). These first three properties of the numerosity representation likely underlie better discriminability of small than large numerosities (14, 15). The properties of the object size representation differ considerably from those of the numerosity representation, suggesting that small object sizes may not be far more discriminable than large object sizes. However, visuospatial receptive fields and neural populations with monotonically changing responses to object size (which we do not examine here, and may carry very different information) may also contribute to object size perception. Furthermore, neural populations with broader tuning functions do not necessarily hold less-detailed information (16).

Fourth, presentation of objects far from the preferred size suppresses object size-tuned responses below baseline. Such surround suppression is common in visuospatial responses (12). Although we find no similar surround suppression for numerosity-tuned responses, we interpret this distinction with caution. The presented numerosities did not cover the entire tuning function, so responses to larger numerosities may reveal suppressive surrounds. However, macaque studies have covered narrower single-neuron numerosity tuning functions more completely without finding surround suppression (15).

Fifth, object size maps were similar in posterior parietal areas of both hemispheres. On the other hand, numerosity maps were far less clear in the left than right hemisphere. However, we did find some left hemisphere numerosity map organization, and numerosity preferences here were also correlated with object size preferences. As such, we find no evidence of lateralization of object size

processing but evidence of partial lateralization of numerosity processing, as reported previously (17). However, given the relatively small numbers of subjects tested in these studies and the few left-handed subjects tested [one in this study, two in our previous study (9)], this lateralization of numerosity processing may not generalize to the entire population.

Finally, object size and numerosity preferences were correlated where they overlapped. However, the two maps are not coextensive and preferences often changed in different directions along the cortical surface, so these maps are distinct structures.

These differences suggest that distinct mechanisms produce object size- and numerosity-tuned responses. They also demonstrate that the properties of tuning and organization we describe do not result from our methods: Very similar methods can produce different results from different neural populations.

Generalization Across Quantities. We find overlapping maps of object size and numerosity, with correlated response preferences across recording sites. Macaque recordings reveal neurons tuned for numerosity only, line length only, or both quantities together in parietal cortex (8, 18). Although we examine tuning for object size rather than line length, similar mechanisms are likely to be involved here. Although neurons tuned for numerosity and line length do not show correlated preferences, only 14 such neurons were recorded (8, 18). We use 35–145 recording sites per hemisphere, giving far greater statistical power. We do not show whether the same neurons or nearby neurons have correlated object size and numerosity preferences. It is not necessary for the same neurons to process both quantities for their representations to interact.

Associated object size and numerosity representations are evident in perception. Participants cannot independently choose larger or more numerous objects when objects vary in both dimensions (6): Larger objects are seen as more numerous and vice versa.

Object size and numerosity represent different aspects of quantity. Grouping these neural representations may allow cognitive processing to link different aspects of quantity and generalize subsequent quantity processing (5). In that sense, object size and numerosity maps may be considered subdivisions of a general nonsymbolic quantity representation (5, 9). Other quantities may have similarly organized and linked neural representations.

Mechanisms and Models of Quantity Tuning. Several mechanisms might produce responses like those we report. Here we examine possible interpretations of our findings.

Could tuning for both object size and numerosity reflect tuning to a single feature that covaries with both quantities? For example, the area surrounding the dot patterns (the convex hull) increases with object size and often, although not always, increases with numerosity, so could tuning for both features reflect tuning for the convex hull extent or the attentional window needed to attend the stimulus? This alternative hypothesis does not fit our results: Our high-density numerosity stimulus condition groups objects in a dense pattern with a much smaller convex hull yet gives very similar responses to less-dense patterns (9). Similarly, object size changes with numerosity in some numerosity stimuli, so could numerosity tuning and correlated quantity preferences both reflect tuning for object size only? Again, this does not fit our results: Numerosity tuning and maps are found even where either individual object size or total object size does not change with numerosity. Where object size does change with numerosity, it decreases with increasing numerosity, predicting negative correlations between numerosity and object size preferences rather than the positive correlations observed.

Furthermore, the many differences in tuning and map organization suggest that different mechanisms are involved. The ratio of object size and numerosity preferences also differs between hemispheres (even in the same subject), whereas any relationship between tuning and stimulus features would not. Therefore, tuning for a single feature cannot explain both responses.
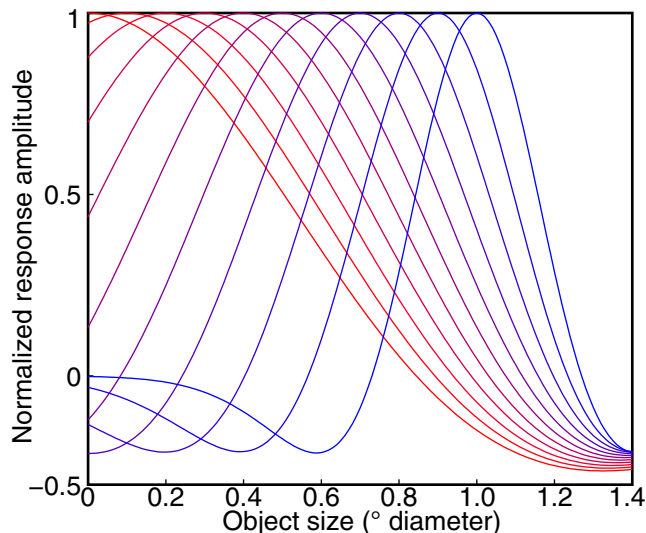

Fig. 4. Object size tuning functions for a range of object size preferences, following average tuning parameters found across all hemispheres.

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We have previously shown that numerosity tuning is stable across stimulus features but not completely invariant (9): Changing relationships between object size and numerosity influence numerosity estimates. This led to the suggestion that numerosity-tuned responses might reflect tuning for a feature that covaries with numerosity in our stimuli (10). We now show correlated object size preferences at the same sites. Therefore, neural populations preferring small numerosities and small sizes may respond more to larger numbers of small objects than smaller numbers of large objects. As such, effects of object size on numerosity estimates do not reflect a covarying feature but rather related tuning preferences for both quantities in the same neural populations.

"Object size" might describe one of several specific features. We do not find similar responses when varying display luminance without changing object size (Fig. S2). We also show that tuning for linear object size (radius, diameter, or circumference) predicts responses better than tuning for areal object size (area or luminance). We do not distinguish tuning for diameter, radius, circumference (which are directly proportional in the circles we use), and spatial frequency. This distinction does not affect our conclusions: All are measures of object size.

Could visuospatial tuning explain object size tuning? Early visual neurons (and voxels) have spatially limited receptive fields and so prefer particular stimulus sizes. However, we find many differences between our object size preferences and visuospatial tuning of earlier size-tuned responses. First, our stimuli present many objects of the same size at different locations, evenly spread across the same stimulus area. Second, most recording sites' visuospatial pRFs are outside our size and numerosity stimulus area. Third, preferred object sizes are far smaller than pRF sizes at the same sites. Last, pRF sizes do not correlate with preferred object sizes.

We also show that our maps do not reflect eccentricity changes (or associated pRF size changes) across a visual field map. First, pRF eccentricities are not correlated with preferred object sizes. Second, object size maps do not share borders with IPS visual field maps. Third, relative positions of object size maps and visual field maps differ between subjects and hemispheres.

Quantity-tuned and visuospatially tuned responses in the same cortical area seem independent. This is in line with macaque results, where about 80% of neurons in quantity-tuned areas show no quantity tuning (8). So, independent intermingled representations of quantity and visual space may exist. On the other hand, interactions between quantity-tuned and visuospatially tuned responses may underlie the cognitive spatial "number line" (5).

Several mechanisms have been proposed to derive numerosity tuning from visuospatial responses (13, 19). We hypothesize that object size tuning could be separated from visuospatial tuning through mechanisms that associate similar receptive field sizes across different visual field positions.

Recent studies show that the numerosity of enumerated patterns affects visual short-term memory capacity, suggesting that the numerosity representation guides attention spread between multiple objects (20). This is in line with the parietal and frontal locations of attention and numerosity processing. The object size representation may similarly guide attention spread within single objects. As visual stimuli attract attention, numerosity- and size-tuned responses may reflect properties of the stimulus or the spread of attention the stimulus generates. Because visual processing guides attention and vice versa, attention may be an inherent component of higher-level visual feature representations.

Conclusions

Because object size and numerosity information help guide human and animal behavior (1–3), straightforward mechanisms to derive these metrics may be selectively advantageous. Extending topographic organization into quantity processing suggests that the computational benefits of topographic wiring efficiency (9) apply to both sensory and cognitive systems, providing common organizing principles. Linking cognitive representations in related feature maps may support increasingly abstract cognition and share processing resources between related cognitive concepts.

1. Cantlon JF, Brannon EM (2007) Basic math in monkeys and college students. *PLoS Biol* 5(12):e328.
2. Woodruff G, Premack D, Kennel K (1978) Conservation of liquid and solid quantity by the chimpanzee. *Science* 202(4371):991–994.
3. Dehaene S, Spelke E, Pinel P, Stanescu R, Tsivkin S (1999) Sources of mathematical thinking: Behavioral and brain-imaging evidence. *Science* 284(5416):970–974.
4. Burr D, Ross J (2008) A visual sense of number. *Curr Biol* 18(6):425–428.
5. Walsh V (2003) A theory of magnitude: Common cortical metrics of time, space and quantity. *Trends Cogn Sci* 7(11):483–488.
6. Hurewitz F, Gelman R, Schnitzer B (2006) Sometimes area counts more than number. *Proc Natl Acad Sci USA* 103(51):19599–19604.
7. Nieder A, Miller EK (2004) A parieto-frontal network for visual numerical information in the monkey. *Proc Natl Acad Sci USA* 101(19):7457–7462.
8. Tudusciuc O, Nieder A (2007) Neuronal population coding of continuous and discrete quantity in the primate posterior parietal cortex. *Proc Natl Acad Sci USA* 104(36):14513–14518.
9. Harvey BM, Klein BP, Petridou N, Dumoulin SO (2013) Topographic representation of numerosity in the human parietal cortex. *Science* 341(6150):1123–1126.
10. Gebuis T, Gevers W, Cohen Kadosh R (2014) Topographic representation of high-level cognition: Numerosity or sensory processing? *Trends Cogn Sci* 18(1):1–3.
11. Dumoulin SO, Wandell BA (2008) Population receptive field estimates in human visual cortex. *Neuroimage* 39(2):647–660.
12. Zuiderbaan W, Harvey BM, Dumoulin SO (2012) Modeling center-surround configurations in population receptive fields using fMRI. *J Vis* 12(3):10.
13. Dehaene S, Changeux JP (1993) Development of elementary numerical abilities: A neuronal model. *J Cogn Neurosci* 5(4):390–407.
14. Piazza M, Izard V, Pinel P, Le Bihan D, Dehaene S (2004) Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron* 44(3):547–555.
15. Nieder A, Miller EK (2003) Coding of cognitive magnitude: Compressed scaling of numerical information in the primate prefrontal cortex. *Neuron* 37(1):149–157.
16. Sereno AB, Lehky SR (2011) Population coding of visual space: Comparison of spatial representations in dorsal and ventral pathways. *Front Comput Neurosci* 4:159.
17. Cohen Kadosh R, et al. (2007) Virtual dyscalculia induced by parietal-lobe TMS impairs automatic magnitude processing. *Curr Biol* 17(8):689–693.
18. Tudusciuc O, Nieder A (2009) Contributions of primate prefrontal and posterior parietal cortices to length and numerosity representation. *J Neurophysiol* 101(6):2984–2994.
19. Dakin SC, Tibber MS, Greenwood JA, Kingdom FA, Morgan MJ (2011) A common visual metric for approximate number and density. *Proc Natl Acad Sci USA* 108(49):19552–19557.
20. Knops A, Piazza M, Sengupta R, Eger E, Melcher D (2014) A shared, flexible neural map architecture reflects capacity limits in both visual short-term memory and enumeration. *J Neurosci* 34(30):9857–9866.
21. Winawer J, Horiguchi H, Sayres RA, Amano K, Wandell BA (2010) Mapping hV4 and ventral occipital cortex: The venous eclipse. *J Vis* 10(5):1.
22. Brainard DH (1997) The Psychophysics Toolbox. *Spat Vis* 10(4):433–436.
23. Piazza M, Fumarola A, Chinello A, Melcher D (2011) Subitizing reflects visuo-spatial object individuation capacity. *Cognition* 121(1):147–153.
24. Teo PC, Sapiro G, Wandell BA (1997) Creating connected representations of cortical gray matter for functional MRI visualization. *IEEE Trans Med Imaging* 16(6):852–863.
25. Wandell BA, Chial S, Backus BT (2000) Visualization and measurement of the cortical surface. *J Cogn Neurosci* 12(5):739–752.
26. Nestares O, Heeger DJ (2000) Robust multiresolution alignment of MRI brain volumes. *Magn Reson Med* 43(5):705–715.
27. Dougherty RF, et al. (2003) Visual field representations and locations of visual areas V1/2/3 in human visual cortex. *J Vis* 3(10):586–598.
28. Yacoub E, Hu X (2001) Detection of the early decrease in fMRI signal in the motor area. *Magn Reson Med* 45(2):184–190.
29. Harvey BM, Dumoulin SO (2011) The relationship between cortical magnification factor and population receptive field size in human visual cortex: Constancies in cortical architecture. *J Neurosci* 31(38):13604–13612.
30. Chumbley J, Worsley K, Flandin G, Friston K (2010) Topological FDR for neuroimaging. *Neuroimage* 49(4):3057–3064.
31. Friston KJ, et al. (1998) Event-related fMRI: Characterizing differential responses. *Neuroimage* 7(1):30–40.
32. Swisher JD, Halko MA, Merabet LB, McMains SA, Somers DC (2007) Visual topography of human intraparietal sulcus. *J Neurosci* 27(20):5326–5337.

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